



<http://www.biodiversitylibrary.org>

Proceedings of the Entomological Society of Washington.

Washington, etc. :Entomological Society of Washington

<http://www.biodiversitylibrary.org/bibliography/2510>

v 87 1985: <http://www.biodiversitylibrary.org/item/54866>

Page(s): Page 510, Page 511, Page 512, Page 513, Page 514, Page 515, Page 516, Page 517, Page 518, Page 519, Page 520, Page 521, Page 522, Page 523, Page 524, Page 525, Page 526

Contributed by: Smithsonian Institution Libraries

Sponsored by: Smithsonian

Generated 30 May 2011 3:51 AM

<http://www.biodiversitylibrary.org/pdf3/006860100054866>

This page intentionally left blank.

tonematidae: Nematoda) can infest and kill up to 20% of the adults (Montague and Jaenike, 1985). Predation, relative resource separation, and competitive asymmetries that constantly fluctuate are thus major factors maintaining the coexistence of insect competitors.

ACKNOWLEDGMENTS

I thank Jake Lehn for allowing me to collect flies and mushrooms from the Binghamton Camping and Hunting Club's preserve. Donnajean Rogers and Duncan Safford were very hospitable during my stay in Vermont. John Jaenike, Frank Ramberg, Robert Mangan, and D. C. Darling made valuable comments on the manuscript. This research was done while I was an M.A. student in the Biological Sciences Department at the State University of New York at Binghamton and was supported by a Sigma Xi Grant-in-Aid of Research to myself and NSF grant DEB 80-08574 to John Jaenike.

LITERATURE CITED

- Anderson, R. S. 1982. Resource partitioning in the carrion beetle (Coleoptera: Silphidae) fauna of southern Ontario: Ecological and evolutionary considerations. *Can. J. Zool.* 60: 1314-1325.
- Atkinson, W. D. and B. Shorrocks. 1981. Competition on a divided and ephemeral resource: A simulation model. *J. Anim. Ecol.* 50: 461-471.
- Beaver, R. A. 1977. Non-equilibrium 'island' communities: Diptera breeding in dead snails. *J. Anim. Ecol.* 46: 783-798.
- Buxton, P. A. 1960. British Diptera associated with fungi. III. Flies of all families reared from about 150 species of fungi. *Entomol. Mon. Mag.* 96: 61-94.
- Fellows, D. P. and W. B. Heed. 1972. Factors affecting host plant selection in desert-adapted cactiphilic *Drosophila*. *Ecology* 53: 850-858.
- Fogelman, J. C. and B. Wallace. 1980. Temperature-dependent development and competitive ability of three species in the *Drosophila affinis* subgroup. *Am. Midl. Nat.* 104: 341-351.
- Fogelman, J. C., W. T. Starmer, and W. B. Heed. 1981. Larval selectivity for yeast species by *Drosophila mojavensis* in natural substrates. *Proc. Nat. Acad. Sci.* 78: 4435-4439.
- Grimaldi, D. A. 1983. Ecology and competitive interactions of four coexisting species of mycophagous *Drosophila*. M.A. thesis, State University of New York at Binghamton.
- Grimaldi, D. A. and J. Jaenike. 1984. Competition in natural populations of mycophagous *Drosophila*. *Ecology* 65: 1113-1120.
- Hackman, W. and M. Meinander. 1979. Diptera feeding as larvae on macrofungi in Finland. *Ann. Zool. Fenn.* 16: 50-83.
- Hanski, I. and H. Koskela. 1977. Niche relations among dung-inhabiting beetles. *Oecologia* 28: 203-231.
- Hinton, H. E. 1981. *Biology of insect eggs*. 3 volumes, Pergamon Press, Oxford.
- Horn, H. S. and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53: 749-752.
- Jaenike, J. and D. Grimaldi. 1983. Genetic variation for host preference within and among populations of *Drosophila tripunctata*. *Evolution* 37: 1023-1033.
- Jaenike, J., D. Grimaldi, A. E. Sluder, and A. L. Greenleaf. 1983. Alpha-amanitin tolerance in mycophagous *Drosophila*. *Science* 221: 165-167.
- Kambysellis, M. P. and W. B. Heed. 1971. Studies of oogenesis in natural populations of Drosophilidae. I. Relation of ovarian development and ecological habitats of the Hawaiian species. *Am. Nat.* 105: 31-49.
- Kearney, J. N. 1982. Selection and utilization of natural substrates as breeding sites by woodland *Drosophila* spp. *Entomol. Exp. Appl.* 33: 31-38.
- Kimura, M. T. 1980. Evolution of food preferences in fungus-feeding *Drosophila*: An ecological study. *Evolution* 34: 1009-1018.
- Kneidel, K. 1983. Fugitive species and priority during colonization in carrion-breeding Diptera communities. *Ecol. Entomol.* 8: 163-169.

- Lacy, R. C. 1984. Ecological and genetic responses to mycophagy in Drosophilidae (Diptera). In Wheeler, Q. and M. Blackwell, eds., Fungus/insect relationships: Perspectives in ecology and evolution. Columbia U. Press.
- Mangan, R. L. 1978. Competitive interactions among host plant specific *Drosophila* species. Ph.D. dissertation, University of Arizona, Tucson.
- . 1982. Adaptations to competition in cactus breeding *Drosophila*, pp. 257–272. In Barker, J. S. F. and W. T. Starmer, eds., Ecological genetics and evolution: The cactus-yeast-*Drosophila* model system. Academic Press, N.Y.
- Martin, M. M. 1979. Biochemical implications of insect mycophagy. Biol. Rev. 54: 1–21.
- Merrell, D. 1951. Interspecific competition between *Drosophila funebris* and *D. melanogaster*. Am. Nat. 85: 159–169.
- Montague, J. R. and J. Jaenike. 1985. Nematode parasitism in natural populations of mycophagous drosophilids. Ecology 66: 624–626.
- Okada, T. 1963. Caenogenetic differentiation of mouth hooks in drosophilid larvae. Evolution 17: 84–98.
- Peck, S. B. and A. Forsyth. 1982. Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera: Scarabaeidae). Can. J. Zool. 60: 1624–1634.
- Shorrocks, B. and P. Charlesworth. 1980. The distribution and abundance of the British fungal-breeding *Drosophila*. Ecol. Entomol. 5: 61–78.
- . 1982. A field study of the association between the stinkhorn *Phallus impudicus* Pers. and the British fungal-breeding *Drosophila*. Biol. J. Linn. Soc. 17: 307–318.
- Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco.
- Spencer, W. P. 1942. New species in the quinaria group of the subgenus *Drosophila*. Univ. Tex. Publ. 4213: 55–66.
- Sturtevant, A. H. 1921. The North American Species of *Drosophila*. Carnegie Inst. Wash. Publ. 301, 150 pp.
- Throckmorton, L. H. 1962. The problem of phylogeny in the genus *Drosophila*. Univ. Tex. Publ. 6205: 207–343.
- . 1966. The relationships of the endemic Hawaiian Drosophilidae. Univ. Tex. Publ. 6615: 335–396.
- . 1975. The phylogeny, ecology, and geography of *Drosophila*, pp. 421–469. In King, R. C. ed., Handbook of genetics. Vol. 3. Invertebrates of genetic interest. Plenum, N.Y.
- Wieland, T. 1968. Poisonous principles of mushrooms of the genus *Amanita*. Science 159: 946–952.
- Wilkins, W. H. and G. C. M. Harris. 1946. The ecology of larger fungi. V. An investigation into the influence of rainfall and temperature on the seasonal production of fungi in a beechwood and pinewood. Ann. Appl. Biol. 33: 179–188.

RECONSTITUTION OF THE TRIBES ULOMINI AND TRIBOLIINI
FOR NORTH AND CENTRAL AMERICA
(TENEBRIONIDAE; COLEOPTERA)

JOHN T. DOYEN

University of California, Berkeley, California 94720.

Abstract.—The tribes Ulomini and Triboliini are redefined, based on external and internal characters of adults and immatures. New World Ulomini include *Alegoria* Laporte, *Antimachus* Gistel, *Apteruleda* Gebien, *Apteruloma* Gebien, *Eutochia* LeConte, *Metabolocerus* Bates, *Pheres* Champion, *Uleda* Laporte and *Uloma* Latreille. *Uloma carolynae* from southern Mexico is newly described. Triboliini include *Aesymnus* Champion, *Latheticus* Waterhouse, *Lyphia* Mulsant and Rey, *Metulosonia* Bates, *Mycotrogus* Horn, *Palorus* Mulsant, *Tharsus* LeConte, *Tribolium* Macleay and *Ulosonia* Laporte.

As constituted in present catalogues the tribe Ulomini is strongly composite, containing taxa representing at least four distinct lineages. From the North American fauna Doyen (1984) removed *Adelina* Dejean, *Sitophagus* Mulsant, *Gnato-cerus* Thunberg, *Doliopines* Horn, *Doliodesmus* Spilman, *Mophis* Champion, and *Cynaenus* LeConte to Diaperini, as the subtribe Adelinina. *Alphitobius* Stephens and *Metaclisa* Jaquelin du Val properly belong to Tenebrionini (Doyen and Tschinkel, 1982; Tschinkel and Doyen, 1980). *Adelonia* Laporte (= *Merotemnus* Horn; Spilman, 1961a), sometimes included in Ulomini should be placed in Belopini (Doyen and Tschinkel, 1982). Most of the remaining "ulomine" genera, related to *Tribolium* and *Palorus*, should be placed in a separate tribe, Triboliini, as detailed below. Ulomini is then restricted to a relatively small group of genera related to *Uloma*. In this sense Ulomini comprises a rather uniform assemblage, characterized by several distinctive synapomorphies (see Doyen and Tschinkel, 1982, and below). This arrangement corresponds to that of Reitter (1917), who restricted the European Ulomini to *Uloma*.

Ulomini and Triboliini are included in the tenebrionoid lineage of Doyen and Tschinkel. This lineage is defined principally by the presence of a spermatheca derived from the bursa copulatrix, and is variable in most other features.

Most characters shared by Ulomini and Triboliini are generalized features distributed widely in the tenebrionoid lineage. These include: lacinia with uncus; epipharynx symmetrical or nearly so; tentorium with bridge posterior, not arched; wing with large recurrent cell, short apical membrane; aedeagus not inverted; ovipositor with subequal coxite and paraproct, coxite with four subequal lobes; defensive reservoirs with nonannulate walls, collecting ducts arranged in a basal line.

Possible synapomorphies linking Ulomini and Triboliini include enlargement

of the defensive reservoirs with a distinct basomedial pouch and closure of the mesocoxal cavities by the apposed mesosternum and metasternum. Reservoir enlargement is, however, an exceedingly common feature, which has occurred independently many times, judging from differences in details of configuration (Tschinkel and Doyen, 1980). More specifically, elongate reservoirs with basomedial pouches occur in Helopini and Cnodalonini as well as Ulomini and Triboliini. It may also be pointed out that relatively small reservoirs with broad openings occur in both Ulomini (*Antimachus*) and Triboliini (*Palorus*). Presumably this is a plesiomorphic condition, which admits the possibility that gland enlargement occurred independently. The other potential synapomorphy, closure of the mesocoxal cavities by the sterna, also occurs more widely, most notably in Hypophloeini and some genera of Diaperini.

Opposed to these few similarities are numerous differences between both adult and larval Ulomini and Triboliini. In adult Ulomini the preapical antennal segments bear large placoid sensoriae, with compound (tenebrionoid) sensoriae on only the apical segment. The ligula is sclerotized, the labroclypeal membrane is often exposed, and the seventh abdominal tergite usually forms a pygidium. In larval Ulomini the mandibular incisor is trilobed, the mala apically incised, the hypopharyngeal sclerome produced anteriorly as a flat process, and the second antennal segment bears a C-shaped sensorium. The abdominal pleura are reduced and the ninth tergite is parabolic, concealing the anus and ninth sternite.

In adult Triboliini placoid sensoriae are never present on the antennae, and compound sensoriae are present only in *Ulosonia* and related genera. The ligula is membranous and the labroclypeal membrane and the seventh tergite are concealed. In larvae the mandibular incisor is bilobed, the mala entire, the hypopharyngeal sclerome simple, U-shaped (absent in some *Tribolium*; Hayashi, 1966: 16), and the second antennal segment bears a lens-shaped sensorium at its apex. Abdominal pleura are evident, and the ninth tergite is only moderately larger than the sternite, and bears a pair of short, pointed urogomphi.

Most of these differences result from apomorphic conditions in Ulomini. When these features occur elsewhere, it is in such remote groups that convergence is almost certain. For example, placoid sensoriae occur outside Ulomini in Scotobiini and *Ammophorus* (Medvedev, 1977). The unusual larval hypopharyngeal sclerome, lack of pleural membranes and paraboloid 9th tergite have counterparts in Alleculinae (Hayashi, 1966; Watt, 1974). Most other features of Ulomini are plesiomorphic, and more precise phylogenetic affinities cannot be specified, though some characteristics of the ovipositor and defensive reservoirs suggest relationship to Helopini and Opatrini (Doyen and Tschinkel, 1982).

In contrast, most Triboliini are clearly similar to Tenebrionini. Important shared characters include: configuration of the internal female reproductive tract and ovipositor; similar wing venation; similar mouthparts (lacinia with uncus; mandibular molas simple or carinate) (adults); ninth abdominal tergite with short, pointed urogomphi (larvae). However, most of these features are probably plesiomorphic.

The most significant differences between Triboliini and Tenebrionini appear to be: 1) the enlargement of the defensive reservoirs (very short, eversible pouches in Tenebrionini); 2) closure of the mesocoxal cavities by the apposed sterna (closed by epimeron in most Tenebrionini); 3) larval antenna with a lens-shaped sensoria

(C-shaped in Tenebrionini); 4) 9th abdominal tergite produced as paired urogomphi (single, medial spine-like process or unmodified in Tenebrionini, except *Tenebrio*).

Most North American Ulomini (s.s.) have the labroclypeal membrane exposed, making it impossible to identify them in existing keys. The following changes in Arnett's (1960) key will assist with identification, until a new key can be devised.

- 2(1). Epistoma without a membranous margin or a membranous band between it and labrum 3
 Epistoma with a membranous margin or a membranous band between it and labrum 2a
- 2a(2). Middle and hind tibiae bearing a longitudinal, finely crenulate carina on the outer (dorsal) margin Diaperini
 Middle and hind tibiae lacking carina on outer margin 2b
- 2b(2a). Seventh abdominal tergite partially exposed as pygidium; mesocoxal cavities closed laterally by sternites; fore tibiae usually with serrate outer (dorsal) margins Ulomini, new sense
 Seventh tergite concealed by elytra; mesocoxal cavities closed by epimeron; fore tibiae with nonserrate outer (dorsal) margins 21
- 10(9). Scutellum small; elytra without scutellar stria; anterior striae non-parallel Phrenapatini
 Scutellum large; elytra with scutellar stria; anterior striae parallel Triboliini

Tribe Ulomini, NEW SENSE

Ulomiens Mulsant, 1854, 1856.

Alegorides Lacordaire, 1859.

Ulomides vrai Lacordaire, 1859 (in part).

Ulomini Reitter, 1917; Gebien, 1938-42 (in part); Skopin, 1978; Kwieton, 1982.

Uloimomorpha Skopin, 1964.

Adult.—Small to large (3-25 mm), elongate to broadly oval, flattened to subcylindrical. Eyes moderately large, anteriorly emarginate or absent (*Typhuloma*); antennae gradually clavate, apical 5-8 segments bearing large placoid sensoriae (exception, *Aphthora*); apical segment with compound (tenebrionoid) sensoriae; labrum transverse, constricted at base; labroclypeal membrane exposed or concealed; mandibles with molas nonstriate, coarsely ridged in *Aphthora*; right mola weakly convex, surface simple or bluntly lobed; left mola concave, complexly lobed; lacinia with 1-2 enlarged apical unci (exception, *Aphthora*); mentum often sexually dimorphic, subtrapezoidal to cordate or oval, flat or weakly convex in females, broadly oval, enlarged and concave, frequently setose in males; ligula sclerotized; labial palp subcylindrical or enlarged, flattened in some males; tentorium with bridge posterior, not arched. Apical membrane 0.20-0.35 wing length. Procoxal cavities closed internally; protibia usually modified in males; mesocoxal cavities closed laterally by sterna or barely open (some *Uloma*); 7th abdominal tergite usually exposed as heavily sclerotized pygidium. Ovipositor with gonostyles lateral, small or moderate in size; coxite about as long as paraproct, with 4 subequal lobes. Internal female reproductive tract with long, thin, branched and tightly coiled spermatheca at base of accessory gland. Defensive reservoirs short, saccate,

with common volume (*Antimachus*) or long tubular, with basomedial pouches and without common volume; reservoir walls without annular folding; secretory tissue drained by basal line of ducts. Aedeagus with tegmen dorsal; median lobe adnate.

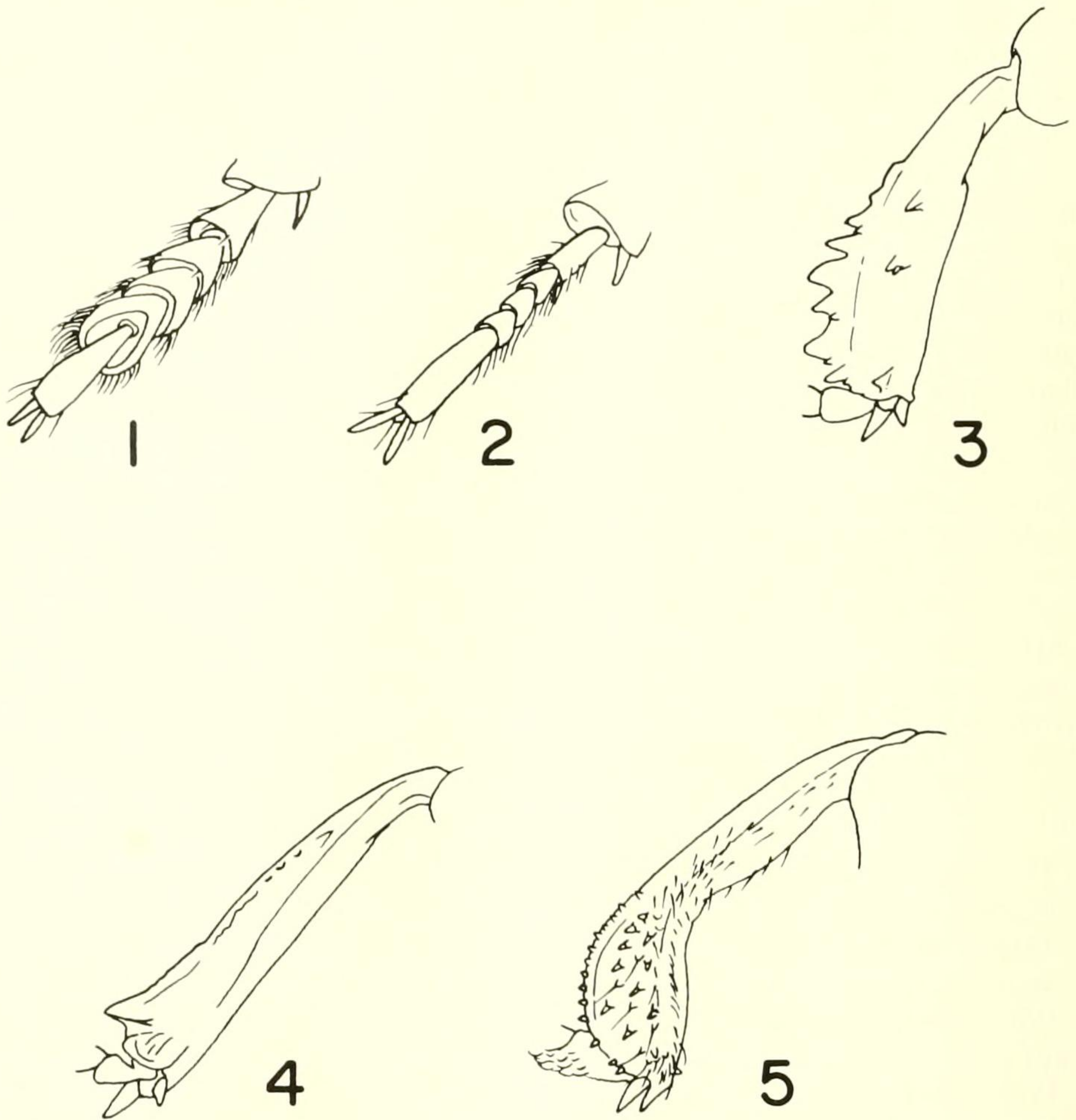
Larva.—Subcylindrical, sides subparallel; moderately to strongly sclerotized and pigmented.

Antenna with second segment about 2.0–2.5 × length of basal, bearing C-shaped sensoria near apex; third segment a digitate process, about ¼ length of second. Labrum transversely ovate; epipharyngeal masticatory processes simple single teeth, slightly asymmetrical. Mandibles with trilobed incisors or left bilobed with subapical tooth; right mola with two coarse, transverse grooves; left mola concave, with strongly prominent anterior margin. Maxilla with mola incised apically, bearing 2 rows of spines. Hypopharyngeal sclerome with base projecting anterad as stout, flattened process or unmodified (*Aphthora*); thoracic legs slender, similar in structure, sparsely set with short, stout spinose setae. Abdomen with pleural sutures obscure, indicated by folds on segments 1–7; greatly reduced or absent on segment 8; ninth tergite large, parabolic, weakly bilobed (*Oligocara*; Cekalovich & Morales, 1974) or produced as single apical and several subapical processes (*Alegoria*; Spilman, 1978); ninth sternite reduced, anus concealed beneath 8th sternite; pygopods absent. Spiracles annular.

KEY TO THE GENERA OF ULOMINI OF
NORTH AND CENTRAL AMERICA

1. Tarsi with penultimate segment flattened, expanded, with last segment inserted dorso-basally (Fig. 1) *Alegoria* Laporte
- Tarsi with penultimate segment subcylindrical, not expanded beneath last segment, which is articulated apically (Fig. 2) 2
2. Protibia with outer (dorsal) apical margin coarsely serrate (Fig. 3)
..... *Uloma* Latreille (in part)
- Protibia with outer (dorsal) margin straight or simply curved, sometimes bearing coarse spines (Figs. 4, 5) never serrate 3
3. Clypeus separated from frons by visible strip of membrane; head without horns 4
- Clypeofrontal membrane concealed beneath frons; males with large medial horn on head *Antimachus* Gistel
4. Metasternal length about one half mesocoxal diameter or less; protibia of males abruptly bent at apical third (Figs. 5, 7) 5
- Metasternal length subequal to mesocoxal diameter; protibia straight or arcuate (as in Fig. 4) 6
5. Eighth interval produced apically as a rounded crest supertending the enlarged punctures of the epipleural stria *Eutochia* LeConte
- Eighth interval not produced as a crest; epipleural punctures subequal to those of other striae *Uloma* Latreille (in part)
6. Epipleuron narrowing gradually to elytral apex (as in Fig. 10); anterior margin of clypeus convex *Pheres* Champion
- Epipleuron terminating abruptly well before elytral apex (as in Fig. 11); clypeus straight or concave *Uleda* Laporte

Besides the North and Central American genera included in the key above, the



Figs. 1-5. Generic characters, Ulomini. 1, 2, Tarsi, dorsal. 1, *Alegoria*. 2, *Uloma*. 3-5, Forelegs, posterior. 3, *Uloma longula* LeConte. 4, *Antimachus* species. 5, *Eutochia picea* Melsheimer.

Ulomini should include *Oligocara* Solier, *Apteruleda* Gebien, *Metabolocerus* Bates, *Apteruloma* Gebien (South America); *Achthosus* Pascoe; *Cneocnemis* Gebien (Oriental); and *Typhuloma* Lea (Australia). Probably such genera as *Macruloma* Pic, *Pycnuloma* Fairmaire, etc., belong in Ulomini in the restricted sense, but I have not made examinations.

Phtora (Palearctic) Mulsant (= *Cataphronetis* Lucas; see Spilman, 1966) strongly resembles *Uloma* in external appearance, but differs markedly in mouthpart configuration. The mandibles have undifferentiated, flattened molars, the lacinia lacks an uncus and the labrum is transverse, without a marked basal constriction. In *Phtora* the tentorial bridge is moderately arched, the antennae bear stellate sensoriae, and the wing venation differs from that of Ulomini (s.s.). Finally, *Phtora* inhabits loose, sandy soil substrates, while most Ulomini are confined to well-rotted wood. Several important internal structures of *Phtora* are undescribed, and

its phyletic relationships are unclear. I have not examined *Erelus* Mulsant & Rey, but from Lacordaire's description it may be close to *Phtora*.

Aphthora rufipes Sharp and *Ulomotypus laevigatus* Brown are likewise of uncertain taxonomic position. While their larvae have the 9th tergite paraboloid, the pleurosternal sutures are distinct. The hypopharyngeal sclerome lacks the anterior process of other Ulomini (Watt, 1974). Adults superficially resemble *Uloma*, and, like Ulomini, have the labrum constricted at the base and, in *Aphthora*, have the ligula sclerotized. However, they lack placoid antennal sensoriae, have the mandibular molars coarsely ridged, and lack an uncus on the lacinia. *Ulomotypus* is further distinguished by having the procoxal cavities open internally, by lacking the transverse bridge of the tentorium and by the inverted aedeagus.

If true Ulomini, these genera would be the most primitive members of the tribe. More likely the similarity to Ulomini in adult body shape and in configuration of the larval abdominal apex represent convergences deriving from similar rotting wood habitats. The coarsely ridged mandibles occur otherwise only in Phrenapatini, but that tribe differs in numerous other adult and larval characters. Most of the other features of *Ulomotypus* and *Aphthora* are generalized and their taxonomic relationships are unclear.

Several genera deviate in one or more characters. *Typhuloma* lacks eyes, while in *Alegoria* and *Antimachus* the elytra conceal the 7th abdominal tergite and the labroclypeal membrane is concealed. In *Alegoria* the penultimate tarsal segments are enlarged beneath the terminal segment. In *Antimachus* the defensive reservoirs are small relative to body size, with broad exits. This configuration occurs in distantly related members of various tribes (see Tschinkel and Doyen, 1980, Fig. 10), and is probably a retained primitive characteristic in *Antimachus*. In other features these genera are unremarkable.

Considerable variation exists among species of *Eutochia*. In *E. picea* LeConte the metasternal length is subequal to the mesocoxal diameter, the 9th elytral intervals are prominently crested above a row of very large punctures just before the apex, and the enlarged mentum of males is broadly oval, slightly concave and covered with flattened setae. This last modification is similar to that of many species of *Uloma*. In *E. pulla* Erichson, *E. atra* Pic and *E. lateralis* Boheman the metasternal length is subequal to the mesocoxal diameter and the elytral apices are unmodified. The mentum of males is small and subtrapezoidal, but the apical segment of the labial palp is enlarged and securiform. These differences suggest that *Eutochia* should be restricted to the New World species. *Cenoscelis* Wollaston, (1867) is then the appropriate name for the Old World species.

The large genus *Uloma* is variable in several features that would be considered diagnostic of the smaller ulomine genera. For example, in most of the New World species the mentum is enlarged in males and modified as described above. In *U. longula* LeConte and *U. impressa* Melsheimer these modifications are absent. Similarly, in most *Uloma* the anterior tibiae are gradually enlarged to the apex, with the outer (dorsal) margin coarsely serrate. In *U. spinipes* Champion and *U. carolinae* Doyen the fore tibiae are apically hooked, with the outer margin weakly serrate or entire. Possibly *Uloma* is composite as now constituted, as predicted by Champion (1886). It is also likely that some of the presently recognized genera (e.g. *Achthosus*) represent specialized lineages derived from *Uloma*. A compre-

hensive study of the entire tribe will be required to resolve these questions. The species described below, together with *U. spinipes* will probably constitute a distinct species group of *Uloma* or a separate genus.

Uloma carolynae, NEW SPECIES

Fig. 6

Male.—Subcylindrical, elongate oval, shining black with piceous appendages and venter. Cranium with punctures about as large as eye facets medially, separated by $\frac{1}{2}$ –1 puncture diameter with an impunctate spot at the epistomal suture, becoming much finer anteriorly and laterally. Epistomum slightly emarginate in dorsal aspect, incised at epistomal suture; suture faint but entire, arcuate; labroclypeal membrane broadly exposed, labrum with disk finely, obscurely and irregularly punctate. Eye barely emarginate, ventral lobe narrower than dorsal. Mentum rugosopunctate, flat, about 1.3 times broader than long, ovate with anterior border narrowly emarginate; labial palp with terminal segment ovate, flattened, aboral surface concave.

Pronotal disk with punctures about $\frac{2}{3}$ size eye facets, separated by about 1–2 puncture diameters; lateral borders arcuate, more strongly so in anterior $\frac{1}{3}$, narrowly margined; anterior border nearly straight in dorsal view, anterior angles obtuse, rounded; posterior border weakly bisinuate; posterior corners nearly right angled, weakly produced, received in sockets in elytral base. Hypomera rugosopunctate; prosternum rugose, prosternal process with transverse groove posteriorly a short distance beyond coxae just before apex, then abruptly declivous.

Elytral disk at base slightly wider than pronotum with prominent humeri; broadest at about middle; strial punctures round, shallow, 1–1.5 times eye facet diameter in sutural stria, becoming larger posteriorly; about 3 times eye facet diameter in epipleural stria; connected by fine furrows except in epipleural stria; intervals convex, finely, sparsely punctate; epipleuron gradually narrowed to elytral apex.

Mesosternum deeply, sharply concave; metasternal length less than $\frac{1}{3}$ mesocoxal diameter; abdominal sternites finely rugose, with punctures about $\frac{1}{2}$ –1 times eye facet diameter interspersed with exceedingly fine punctures. Fore and middle femora clavate; fore tibia with blunt triangular tooth about $\frac{1}{3}$ from base; apical third strongly curved mesally (Fig. 7), posterior surface with raised lateral margin, mesal subapical tooth and apical flattened projection subtended by row of spinose fulvous setae; middle femur with sparse strip of short stiff, fulvous setae on anteroventral surface; middle tibia (Fig. 8) arcuate, with thickened angulation $\frac{2}{5}$ from base, row of erect, spinose setae running from angulation to apex along posteroventral surface; hind femur weakly arcuate, slightly thicker apically, with band of fulvous setae on anteroventral surface; hind tibia nearly straight with row of erect, spinose setae from just before base to apex.

Female.—Labial palp with last segment subcylindrical; fore tibia slightly thickened about $\frac{1}{3}$ from base, apical $\frac{1}{4}$ bent slightly mesad (Fig. 9), anteroventral margin with row of erect spinose setae from near base to apex; middle tibia without angulate thickening on ventral surface.

Elytral length, 8.8–9.25 mm; greatest elytral width 6.0–6.3 mm; median pronotal length, 4.4–4.9 mm; greatest pronotal width, 5.2–5.6 mm.

Holotype male and female paratype (California Academy of Sciences) from

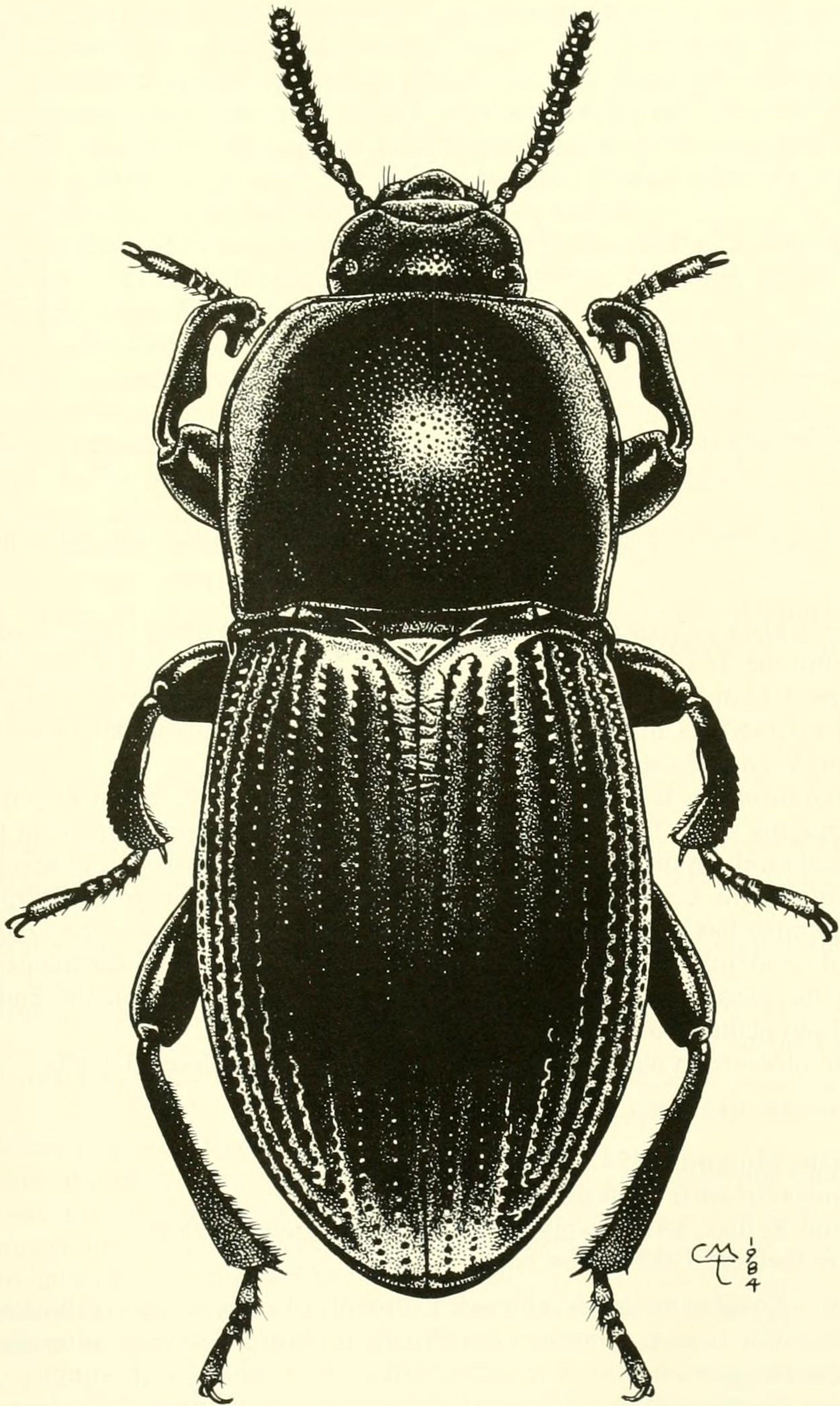
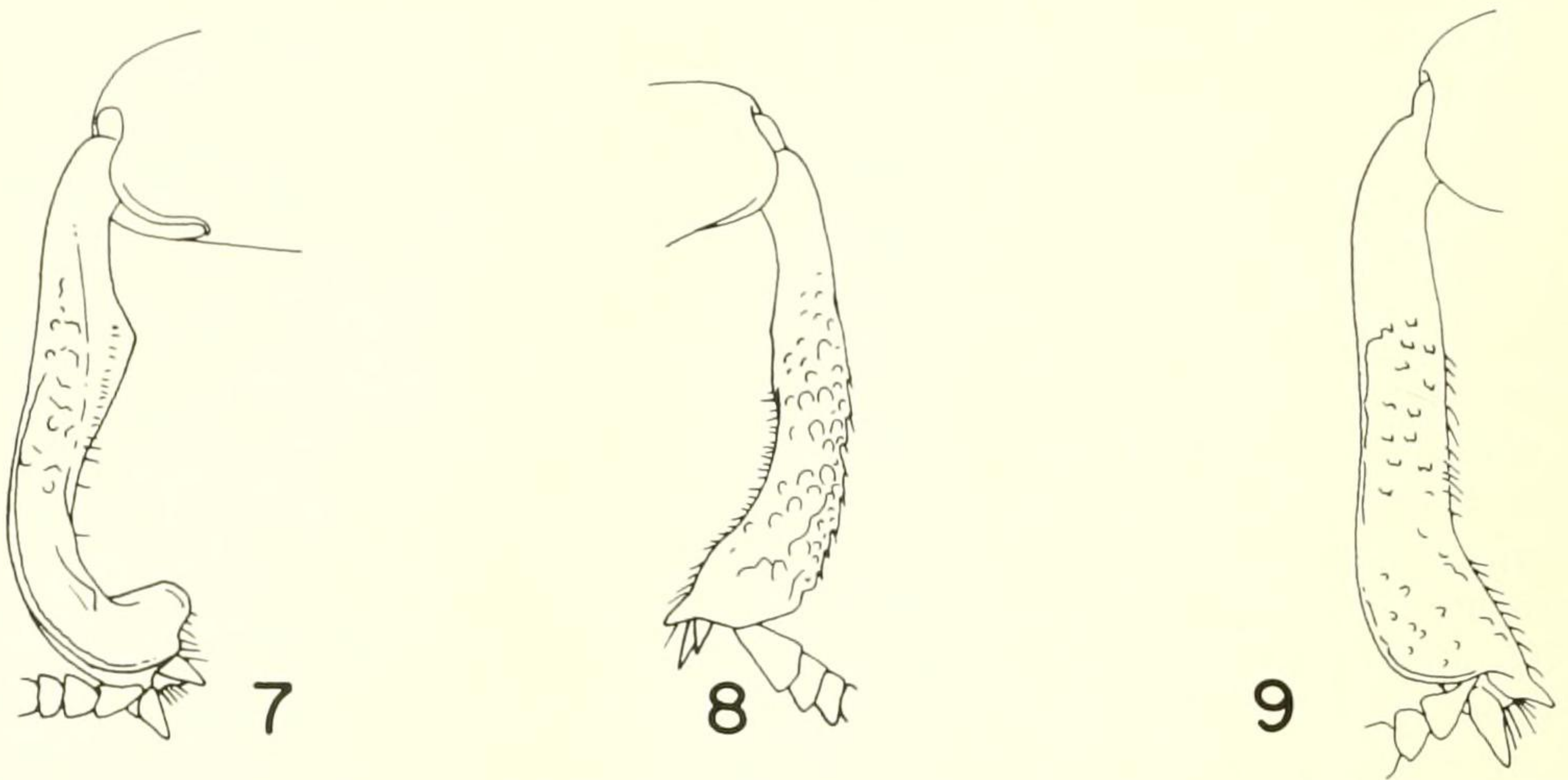


Fig. 6. *Uloma carolinae*, male, habitus.



Figs. 7-9. *Uloma carolynae*. 7, Fore tibia, male. 8, Middle tibia, male. 9, Fore tibia, female.

Mexico, Chiapas-Oaxaca border, 21 km W Rizo de Oro along ridge SE of Cerro Baul, altitude 1615 m, 6-IX-1972. Carolyn Mullinex. In cloud forest. One ♂ paratype, 19 km W Rizo de Oro, Cerro Baul, 1615 m, IV-28-1922. D. E. Breedlove; 1 ♀ paratype, Chiapas, SE side Cerro Tres Picos, montane rain forest, 1524-1829 m, V-28-1972. D. E. Breedlove.

Uloma carolynae is most similar to *U. spinipes* Champion, from which it differs in having the outer foretibial margin entire (denticulate in *spinipes*), in lacking the apical tooth on the middle tibia, and in lacking both the basal and apical teeth on the hind tibia. *U. carolynae* has rows of erect setae on the ventral tibial margins, while *spinipes* has brushes of hairs at the tibial apices. *U. extraordinaria* Spilman (1961b), evidently belongs in the *spinipes* species group. It is distinguished by having the basal protibial tooth very long, narrow and acute in the male, and shorter but acute in the female (Spilman, 1961: figs. 1, 2).

I take pleasure in naming this species for Carolyn Mullinex-Tibbets.

Tribe Triboliini

Triboliens Mulsant, 1854, 1856.

Triboliides (in part) Lacordaire, 1859.

Triboliini Reitter, 1917; Skopin, 1964, 1978; Kwieton, 1982.

Ulomini Gebien, 1938-42 (in part).

Adult.—Small to moderate, elongate to broadly oval, flattened to subcylindrical. Eyes moderate in size, anteriorly emarginate or entire (*Palorus*); antennae gradually clavate or with abrupt 4 segmented club (*Lyphia*), with simple, conical sensoriae, or with compound (tenebrionoid) sensoriae on inner and outer margins of apical 7-8 segments. Labrum subquadrate (*Palorus*) or broadly transverse; labroclypeal membrane concealed; mandibles with molas similar with simple or striate surface; lacinial uncus present or absent; ligula membranous; tentorium with bridge posterior, not arched, or absent (*Palorus*). Mesocoxal cavities closed laterally by sterna; apical membrane less than $\frac{1}{3}$ wing length. Ovipositor with

gonostyles lateral, small; coxite as long or longer than paraproct, with 4 subequal lobes, sometimes poorly defined. Internal female tract with long, thin, tightly coiled spermatheca at base of accessory gland, or with single diverticulum (*Palorus*). Defensive reservoirs short, saccate with broad openings (*Palorus*) or long, saccate with constricted openings; without common volume; reservoir walls without annular foldings; secretory tissue drained by basal field or basal line of ducts. Aedeagus with tegmen dorsal; median lobe free or adnate.

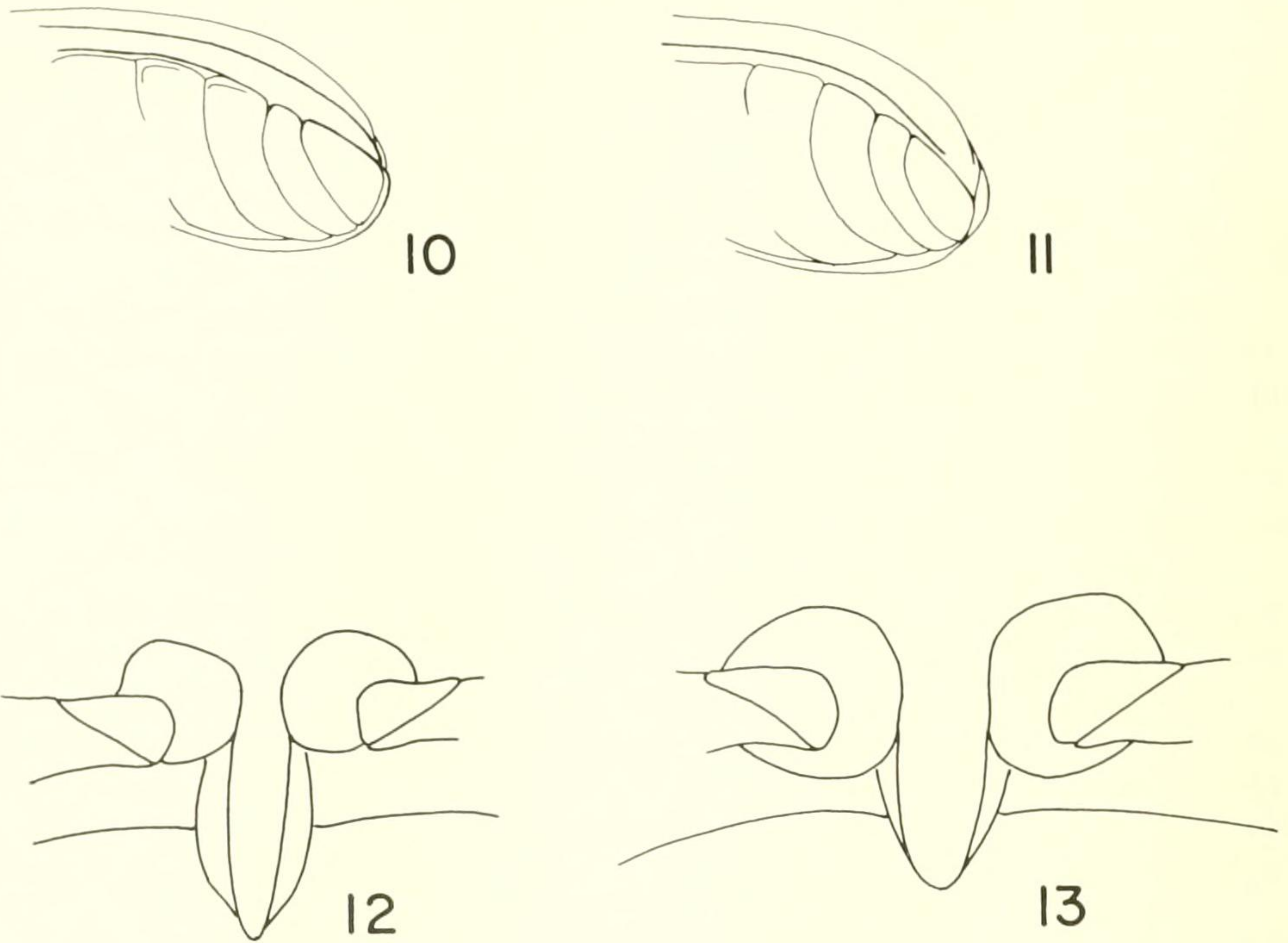
Larva (synthesized in part from Hayashi, 1966; Halstead, 1967a; Van Emden, 1947; Skopin, 1978).—Subcylindrical, slightly flattened ventrally, weakly sclerotized; caudal segments gradually tapering.

Antenna with 2nd segment about 1.25–2.0 × length of basal, bearing apico-medial lens shaped sensoria. Labrum transverse (*Tribolium*) or ovate; epipharyngeal masticatory process of small, single, slightly asymmetrical teeth or undeveloped (*Tribolium*). Mandibles with bilobed incisor; molar lobes strong, projecting, flat or nearly so, sometimes bearing few carinae. Maxilla with mala evenly convex, not incised; finely setose. Hypopharyngeal sclerome concave with base not produced, or absent (*Tribolium*; Hayashi, 1966). Thoracic legs slender, similar in structure, sparsely set with hair-like setae. Abdominal segments with pleural sutures distinct; tergite and sternite 9 subequal; tergite 9 produced as sharply pointed urogomphi; pygopods absent (*Latheticus*; Hayashi, 1966) or present. Spiracles annular.

The following key is modified in part from Spilman, 1962.

KEY TO THE GENERA OF TRIBOLIINI OF
NORTH AND CENTRAL AMERICA

1. Elytral intervals finely carinate *Tribolium* Macleay
- Elytral intervals flat or convex, sometimes with weak carina in eighth interval 2
2. Elytral epipleuron tapering gradually posteriorly, attaining elytral apex (Fig. 10) 3
- Elytral epipleuron ending abruptly well before elytral apex (Fig. 11) *Tharsus* LeConte
3. Antenna with last 4 segments forming distinct, capitate club *Lyphia* Mulsant and Rey
- Antenna gradually clavate 4
4. Middle and hind tibiae arcuately curved *Aesymnus* Champion
- Middle and hind tibiae straight 5
5. Pronotal disk with punctures of two distinct sizes 6
- Pronotal disk with punctures of a single size 8
6. Distance between eye and cardo much less than width of cardo 7
- Distance between eye and cardo greater than width of cardo *Mycotrogus* Horn
7. Prosternal process extending posteriorly beyond procoxae by nearly twice coxal length; apex acute, very narrowly rounded (Fig. 12) *Metulosonia* Bates
- Prosternal process extending posteriorly beyond procoxae by about one coxal length; apex broadly rounded (Fig. 13) *Ulosonia* Laporte
8. Eye round, entirely ventrad of epistomal canthus *Palorus* Mulsant



Figs. 10–13. Generic characters, Triboliini. 10, 11, Apical region of abdomens. 10, *Ulosonia*. 11, *Tharsus*. 12, 13, Prosternal processes. 12, *Metulsonia*. 13, *Ulosonia*.

- Eye reniform, emarginated in dorsal third by epistomal canthus
 *Latheticus* Waterhouse

On the basis of adult features, Triboliini comprises two groups of genera. The *Palorus* “genus group” (Halstead, 1967b) is characterized as follows: labrum subquadrate; lacinia without uncus; eye entire; tentorial bridge absent; defensive glands small, short, saccate with broad openings; bursa copulatrix with single, thick diverticulum (accessory gland?). *Palorus* is introduced to North America; other members of the *Palorus* genus group occur in the Old World (see Halstead, 1967b).

The remaining North American Triboliini are more similar to *Tribolium*, and might be referred to as the “*Tribolium* genus group.” This group is characterized as follows: labrum transverse; lacinia with uncus; eye anteriorly emarginate; tentorial bridge present, posterior, not arched; defensive glands large, elongate; female reproductive tract with both spermatheca and accessory gland.

Although they share a high level of phenetic similarity in external characters of both adults and larvae, the drastic difference between these genus groups in configuration of the female reproductive tract is unusual and suggests that the relationship between these groups deserves further consideration. Such an undertaking would require detailed study of the predominantly Old World fauna of Triboliini, which is beyond the scope of this work.

Among the *Tribolium* genus group, the genera *Ulosonia*, *Metulsonia* and *My-*

cotrogus have striate mandibular molae, the prosternal process extended far posteriorly and received in the deeply concave mesosternum, compound antennal sensoriae and relatively shorter defensive reservoirs with broad openings. In *Lypbia*, *Latheticus*, *Tribolium*, and *Tharsus* the mola is nonstriate, the prosternal process is relatively short, the antennal sensoriae are simple cones (with 2 or more sensory pegs in some *Tribolium*; Roth & Willis, 1951) and the defensive reservoirs are very elongate with constricted openings and basomedian pouches. *Tharsus* is unique among the genera considered here in having the epipleuron ending before the elytral apex, but this character is quite variable in other tribes such as Diaperini. I have been unable to dissect *Aesymnus*, but external features indicate placement in Triboliini.

ACKNOWLEDGMENTS

Some of the specimens required for dissection were provided by T. J. Spilman, Systematic Entomology Laboratory, Agricultural Research Service, Washington, D.C., C. A. Triplehorn, Ohio State University, M. J. D. Brendell, British Museum (Natural History), J. F. Lawrence, Australian National Insect Collection and J. C. Watt, DSIR, Auckland. M. J. D. Brendell made available types of several Central American taxa. Specimens of *Uloma carolynae* were loaned by D. Kavanaugh, California Academy of Sciences. J. C. Watt made available his dissections of *Ulomotypus* and *Aphtora* and provided insights regarding their taxonomic position. Carolyn Mullinex-Tibbets made the illustrations. J. A. Chemsak reviewed an earlier version of the manuscript. The research was supported in part by N.S.F. grant INT 81-14360.

LITERATURE CITED

- Arnett, R. H., Jr. 1960. The beetles of the United States. Catholic University Press, Washington, D.C. ix + 1112 pp.
- Cekalovich, T. and E. Morales. 1974. Descripcion de la larva de *Oligocara nitida* Solier, 1848 (Coleoptera, Tenebrionidae). Bol. Soc. Biol. Concepcion 48: 173-177.
- Champion, G. C. 1886. Biologia Centrali-Americana, Insecta, Coleoptera (Tenebrionidae), vol. 4, pt. 1: 137-264.
- Doyen, J. T. 1984. Reconstitution of the Diaperini of North America, with new species of *Adelina* and *Sitophagus* (Coleoptera: Tenebrionidae). Proc. Entomol. Soc. Wash. 86: 777-789.
- Doyen, J. T. and W. R. Tschinkel. 1982. Phenetic and cladistic relationships among tenebrionid beetles (Coleoptera). Syst. Entomol. 7: 127-183.
- Gebien, H. 1938-42. Katalog der Tenebrioniden, Teil II. Mitt. Muench. Entomol. Ges. 28-32: 370-744 [repaged].
- Halstead, D. G. H. 1967a. Biological studies on species of *Palorus* and *Coelopalorus* with comparative notes on *Tribolium* and *Latheticus* (Coleoptera: Tenebrionidae). J. Stored Prod. Res. 2: 273-313.
- . 1967b. A revision of the genus *Palorus* (sens. lat.) (Coleoptera: Tenebrionidae). Bull. Brit. Mus. (Nat. Hist.) Entomol. 19: 5-148.
- Hayashi, N. 1966. A contribution to the knowledge of the larvae of Tenebrionidae occurring in Japan (Coleoptera: Cucujoidea). Insecta Matsumarana, Suppl. 1: 1-41, 32 pls.
- Kwieton, E. 1982. Revue critique des systèmes récents de la famille des Tenebrionidae (Col.). Acta Mus. Nat. Prague 38(B): 79-100.
- Lacordaire, T. 1859. Histoire naturelle des insectes. Genera des Coléoptères. Tome 5. Roret, Paris. 750 pp.
- Medvedev, G. S. 1977. The taxonomic significance of the antennal sensillae of the darkling beetles. Acad. Nauk SSSR, Trudi Vsesoyuznovo Entomologicheskovo Obschestva 58: 61-86.

- Mulsant, E. 1854. Histoire naturelle des Coléoptères de France, pt. 5, latigènes, pp. 1-396.¹
- . 1856. Histoire naturelle des Coléoptères de France. Tribu des latipennes. Ann. Soc. Linn. Lyon (2)3: 305-471.¹
- Reitter, E. 1917. Bestimmungstabellen europäischer Coleoptera. — 81. Unterfamilien und Tribus der palaeärtischen Tenebrionidae. Wien. Entomol. Zeit. 36: 51-66.
- Roth, L. M. and E. R. Willis. 1951. Hygroreceptors in adults of *Tribolium* (Coleoptera, Tenebrionidae). Jour. Exptl. Zool. 116: 527-570.
- Skopin, N. G. 1964. Die Larven der Tenebrioniden des Tribus Pycnocerini (Coleoptera, Heteromera). Ann. Mus. R. Afr. Cent. Ser. Quart. 127: 1-35.
- . 1978. Tenebrionidae. In Klausnitzer, B. Ordnung Coleoptera (larven). Junk, The Hague. 378 pp.
- Spilman, T. J. 1961a. Remarks on the classification and nomenclature of the American Tenebrionine genus *Adelonia*. Pan-Pac. Entomol. 37: 49-51.
- . 1961b. *Uloma extraordinaria*, a new species from Cuba (Tenebrionidae). Coleopt. Bull. 15: 113-115.
- . 1962. A few rearrangements in the Tenebrionidae, with a key to the genera of the Ulomini and Tenebrionini of America, north of Mexico. Coleopt. Bull. 16: 57-63.
- . 1966. On the generic names *Alphitobius*, *Phtora*, *Clamoris* and *Cataphronetis* (Coleoptera: Tenebrionidae). Proc. Entomol. Soc. Wash. 68: 6-10.
- . 1978. Descriptions of the larva, pupa, and adult of *Alegoria dilatata*, associated with banana plants in the Neotropics (Coleoptera: Tenebrionidae). U.S. Dep. Agr. Coop. Pl. Pest Rep. 3: 47-51.
- Tschinkel, W. R. 1975. A comparative study of the chemical defensive system of tenebrionid beetles. III. Morphology of the glands. J. Morphol. 145: 355-370.
- Tschinkel, W. R. and J. T. Doyen. 1980. Comparative anatomy of the defensive glands, ovipositors and female genital tubes of tenebrionid beetles (Coleoptera). Int. J. Insect Morphol. and Embryol. 9: 321-368.
- Van Emden, F. I. 1947. Larvae of British beetles. VI. Tenebrionidae. Entomol. Mon. Mag. 83: 154-171.
- Watt, J. C. 1974. A revised subfamily classification of Tenebrionidae (Coleoptera). N.Z. J. Zool. 1: 381-452.
- Wollaston, T. V. 1867. Coleoptera Hesperidum, being an enumeration of the coleopterous insects of the Cape Verde Archipelago. London, 285 pp.

¹ From Blackwelder, R. E. 1957. Checklist of the Coleopterous Insects of Mexico, Central America, the West Indies, and South America. U.S. Nat. Mus. Bull. 185: 927-1492.

THE NYMPH OF *BISANCORA RUTRIFORMIS* SURDICK
(PLECOPTERA: CHLOROPERLIDAE)¹

KENNETH W. STEWART AND JEAN A. STANGER

Department of Biological Sciences, North Texas State University, Denton, Texas 76203.

Abstract.—The previously unknown nymph of the stonefly *Bisancora rutriformis* was collected at its type locality, reared, and is described and illustrated herein. Preliminary comparisons, based on similarities of pronotal setation and mouthparts between it and nymphs of the other seven genera of the subfamily Chloroperlinae indicate that *rutriformis* is most closely allied with *Alloperla*. This corroborates relationship of these two genera based on adult genitalia.

In 1978, K. W. Stewart and B. P. Stark began a program to rear and comparatively describe and illustrate the unknown and poorly known nymphs of North American stonefly genera to enable: (1) construction of the first complete generic-level nymph key, and (2) acquisition of new nymphal characters that could be used as additional lines of evidence for phylogenetic analyses of Plecoptera. Since then, they and colleagues have described and illustrated for the first time nymphs in the genera *Calliperla* (Perlodidae) (Szczytko and Stewart, 1984), *Cascadoperla* (Perlodidae) (Szczytko and Stewart, 1979), *Chernokrillus* (Perlodidae) (Stewart and Stark, 1984), *Lednia* (Nemouridae) (Baumann and Stewart, 1980), *Oconoperla* (Perlodidae) (Stark and Stewart, 1982b), *Viehopera* (Peltoperlidae) (Stark and Stewart, 1982a), representative nymphs for all genera in the Peltoperlidae (Stark and Stewart, 1981) and Perlodinae (Stewart and Stark, 1984), and nymphs of the species of *Taeniopteryx* (Fullington and Stewart, 1980).

The only remaining nearctic genera with unknown nymphs are *Hansonoperla* Nelson (Perlidae) (Nelson, 1979) and *Bisancora* Surdick (Chloroperlidae) (Surdick, 1981b). On May 13, 14, 1984, K. W. Stewart and B. Poulton visited Little Rock Crk., Los Angeles Co., Calif., the type locality of *Bisancora rutriformis* Surdick, and adjacent streams in the San Gabriel Mts. They collected the following *B. rutriformis* specimens: (1) 1 mature ♂ nymph, 13 ♂ and 6 ♀, Little Rock Crk., 6.3 mi. S. Hwy. 138 (Pearblossom Hwy.) on Cheeseboro Rd. (2.4 mi. S. Little Rock Dam) 13-IV-1984, and (2) 1 ♀ nymph, 4 ♂ and 2 ♀, Little Rock Crk. between Basin and Sycamore campgrounds, 14-IV-1984. The female nymph was field-reared in a styrofoam ice chest. The following description and figures were prepared from the single male nymph, and nymphal exuvium from the reared female.

With B. P. Stark we are currently engaged in a comparative study of chloro-

¹ Study supported in part by National Science Foundation Grants DEB78-12565, BSR 8308422 and the Faculty Research Fund of North Texas State University.

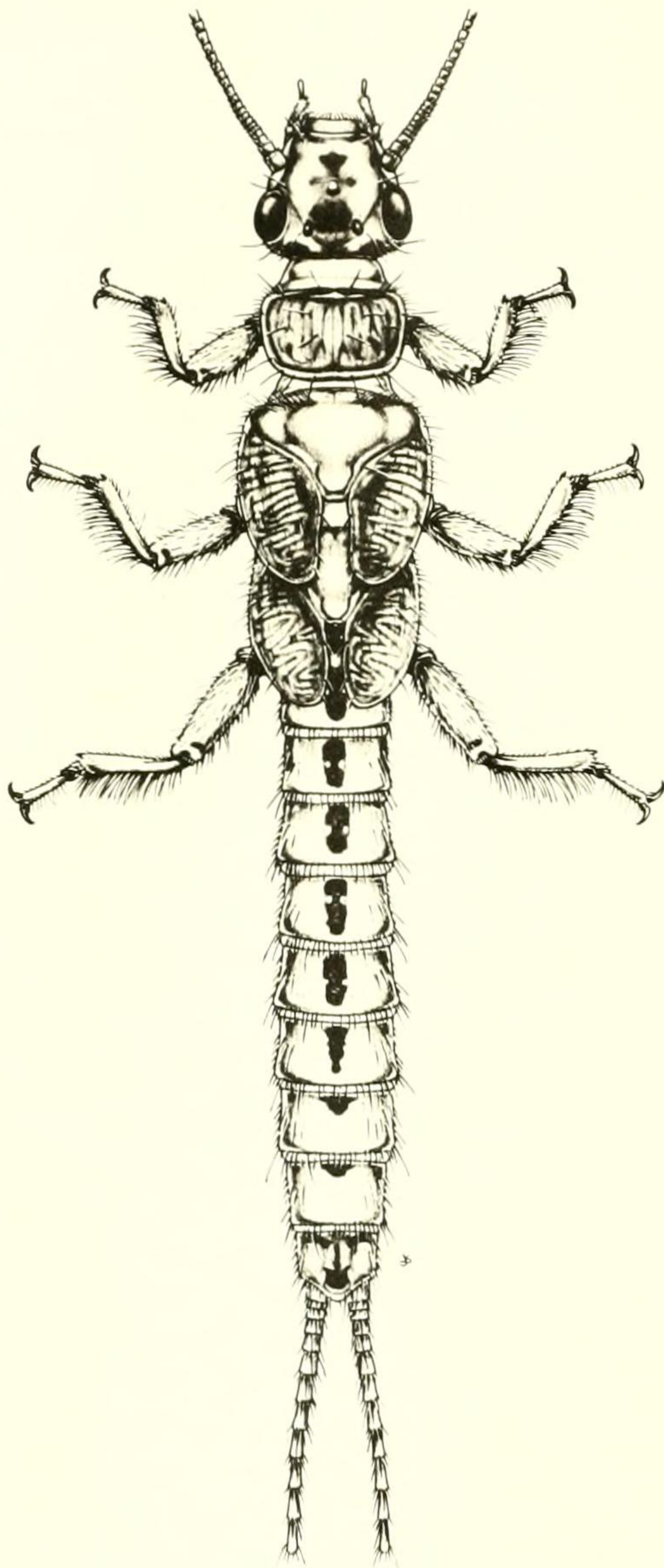


Fig. 1. Nymph habitus of *Bisancora rutriformis*; scale line = 2 mm.

perlinae nymphs, which should help to further elucidate generic relationships in this group. Morphological gaps between several genera are relatively small in all life stages; for example, the epiproct differences (which should carry heavy weight in character analysis) between species of *Bisancora*, *Alloperla* and some *Sweltsa* seem sufficiently subtle to raise questions about their placement in separate genera. A careful comparative study of all life stages is needed for acquisition of additional characters in the group.